

Finding a Resting Place: How Environmental Conditions Influence the Habitat Selection of Resting Batoids

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Abstract.—Many batoid species will form aggregations while resting on the seafloor; however, the environmental variables that drive resting habitat selection behavior, and how it varies among species are not well understood. Bat rays (*Myliobatis californica*), shovelnose guitarfish (*Pseudobatos productus*), and round stingrays (*Urobatis halleri*) have been observed forming heterospecific aggregations. We investigated the effects of substrata type and seafloor water temperature as two likely variables that would influence resting habitat selection for these species. Spatial distribution patterns of individuals were determined via diver-based surveys over two survey seasons (Fall 2013 and Summer 2014) and related to detailed georeferenced habitat maps. While these batoids were found resting on both soft sediment types available, fine-sand was selected by all three species, whereas bat rays were the only one of the three species to select for vegetated-sand. The varying thermal sensitivities of the batoids likely influenced their responses to daily and seasonal temperatures within the study area. During Fall 2013, the three species were most abundant across a narrow temperature range (18.00 – 18.25°C); during Summer 2014, there were higher densities of bat rays in areas where daily maximum seafloor temperature reached 20°C. Each species demonstrated habitat selection decisions that were indicative of balancing tradeoffs between environmental variables. As K-selected, meso-level predators, aggregating in predictable ways can ultimately make batoids more susceptible to fishing and anthropogenic pressures. Therefore, knowledge of how batoids select their resting habitat and how environmental conditions shape distributions may provide managers with opportunities to implement better protection for resting species.

Many non-schooling elasmobranchs have been observed resting in loose aggregations on the seafloor; however, the environmental and biological variables that drive this behavior and how it varies among species are not well understood. An aggregation is defined as a group that forms when individuals seek out suitable conditions or resources, and the individuals within the group respond independently instead of using social cues or behaviors (Heupel and Simpfendorfer 2005). Individuals within the aggregations need to manage the costs (e.g., risk of parasites, competition for resources) and benefits (e.g., predator avoidance, foraging efficiency) associated with being in a group (Romey 1995; Hoare et al. 2004; Jacoby et al. 2012). Therefore, aggregations should form when the benefits outweigh the costs, leading to a potential fitness gain. However, if the costs begin to outweigh the benefits, the habitat may become unfavorable and cause individuals to move.

Elasmobranch aggregations have been observed in highly mobile species such as scalloped hammerhead sharks (*Sphyrna lewini*) and grey reef sharks (*Carcharhinus amblyrhynchos*) (Klimley et al. 1988; Economakis and Lobel 1998; Heupel and Simpfendorfer 2005),

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as well as, non-obligate ram ventilating (intermittently active), demersal species including most batoids such as cowtail stingrays (*Pastinachus sephen*) and reticulate whiprays (*Himantura uarnak*) (Semeniuk and Dill 2006). Most batoids spend a considerable amount of time resting on or in soft substrata, so it is suggested they would choose resting habitats with adequate foraging or refuging opportunities as well as suitable environmental conditions. Therefore, we hypothesized two environmental variables that influence habitat selection decisions for benthic batoid species most likely include substrata type because of their direct association with the seafloor, and water temperature because of their ectothermic physiology. Because these two key environmental variables can vary temporally (i.e., tides, seasons) and spatially (i.e., depth, geographically), some batoid species may periodically aggregate in certain areas when conditions are physiologically or behaviorally advantageous.

When batoids are observed on the seafloor, it is assumed they are resting or potentially foraging. While it can be difficult to observe foraging behaviors without influencing their behavior, observing batoids at rest can be less invasive and used to quantify how substrata type influences resting habitat selection. More susceptible batoids may use unconsolidated sediment substrata (e.g., sand, mud) (White and Potter 2004), because it offers a place for individuals to partially bury to hide from predators while at rest (i.e., refuging). At times, batoids may find suitable benthic habitat for resting, but other variables changing around them, such as temperature, could limit whether individuals choose that substratum or remain in that area.

Temperature is considered one of the key environmental variables influencing elasmobranch distributions, movements, and habitat selection due to its direct effect on physiological functions (Brett 1971; Schmidt-Nielsen 1997; Bernal and Lowe 2015). Warmer temperatures can benefit ectotherms physiologically by increasing rates of physiological processes (i.e., muscle performance, metabolism, digestion); however, if too warm, temperatures may add additional physiological costs by decreasing physiological efficiency (Economakis and Lobel 1998; Hight and Lowe 2007; Di Santo and Bennett 2011b, a). When environmental temperature changes, thermally-insensitive elasmobranchs, those with low Q_{10} s, may be able to better tolerate their chosen resting habitat. In contrast, thermally-sensitive elasmobranchs (high Q_{10} s) may be forced to move to a more thermally suitable habitat (Fangue et al. 2003; Wallman and Bennett 2006; Luongo and Lowe 2018). To compensate, some elasmobranchs behaviorally thermoregulate by shuttling between heterogeneous thermal conditions to gain an energetic advantage (Di Santo and Bennett 2011a; Bernal and Lowe 2015). For example, bat rays (*Myliobatis californica*), lemon sharks (*Negaprion brevirostris*), and Atlantic stingrays (*Dasyatis sabina*) implement a “hunt warm – rest cool” strategy where they forage in warmer waters and rest in comparatively cooler waters to decrease metabolic costs and increase digestive efficiency (Hopkins and Cech 1994; Matern et al. 2000; Di Santo and Bennett 2011b; DiGirolamo et al. 2012).

Because of their meso-predator trophic level, K-selected life history traits, and time spent resting on the seafloor, aggregating in predictable temporal and spatial patterns makes some batoid species particularly vulnerable to overfishing, (Mucientes et al. 2009; Jacoby et al. 2012), emphasizing the need to understand the drivers of habitat selection decisions for resting batoids. Big Fisherman’s Cove (BFC) at Santa Catalina Island is a marine reserve with a high diversity of marine species, including high abundances of elasmobranchs. Bat rays (*Myliobatis californica*), shovelnose guitarfish (*Pseudobatos productus*) (from now on referred to as “shovelnose”), and round stingrays (*Urobatis halleri*) have all been observed aggregating in BFC, yet no studies have been done to determine what mechanisms

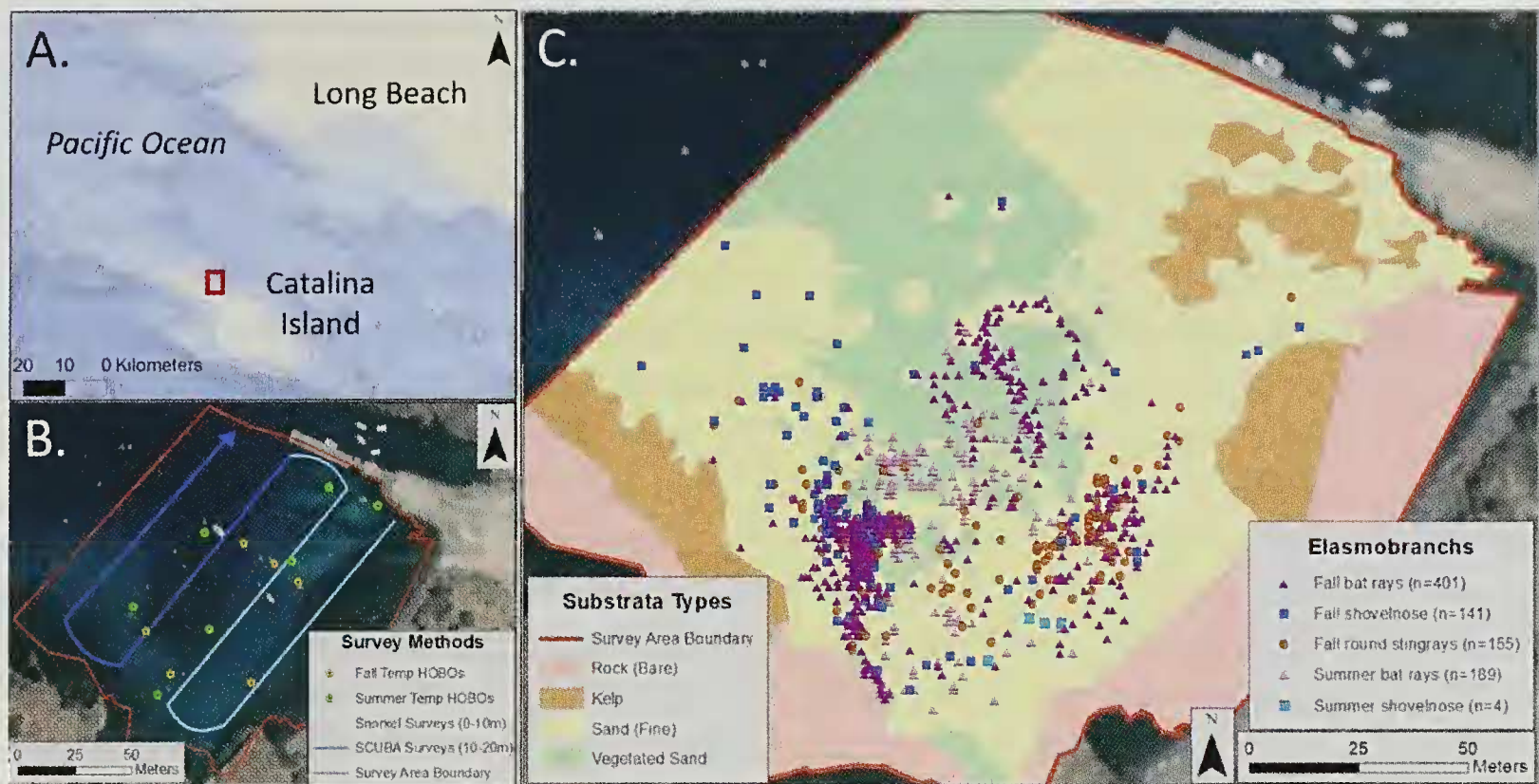


Fig. 1. A) Big Fisherman's Cove (BFC) location at Santa Catalina Island, USA. B) Survey methods for collecting batoid geolocation positions, substrata type, and locations of temperature data loggers. C) Benthic substrata map indicating different substrata classifications within BFC and positional estimates observed for each batoid during Fall 2013 and Summer 2014. Red survey area boundary (panels B and C) indicates extent of daily surveys.

drive these heterospecific aggregations. Therefore, to better understand how these three batoid species form aggregations, the goal of this study was to investigate substrata type and temperature as potential variables that drive their resting habitat selection decisions.

Materials and Methods

Diver-based visual surveys took place in Big Fisherman's Cove (BFC) at Santa Catalina Island off the southern California coast ($33^{\circ} 26' N$, $118^{\circ} 29' W$) (Fig. 1A). Surveys occurred at different times of day in the Fall of 2013 ($n = 11$) and the Summer of 2014 ($n = 10$). Surveys were done using belt transects (width varied depending on daily visibility) that spanned the entire cove area (2.73 ha) (Fig. 1B). Transects extended approximately 165 m from the shoreline in the northwest direction, in depths no deeper than 20 m. Shallow areas (depth: 0-10 m) were surveyed from the surface via snorkeling, while the deeper areas (depth: 10-20 m) were surveyed using SCUBA. During these surveys, geo-positional fixes of all observed resting batoids and the substrata type they were resting on were recorded by a diver positioned directly over top, orthogonal to the animal, using a handheld GPS unit at the surface (Garmin GPSmap 76Cx). For the deeper areas, two divers surveyed 3 m above the seafloor while a snorkeler, connected by rope to the divers, followed from above in order to gather accurate geo-positional fixes of sighted individuals. The rope allowed divers to communicate what substrate and species to record for each positional point via a series of tugs to the snorkeler with the GPS. Geo-positional fixes were not recorded if an observed batoid was swimming to or from the area. In addition, temperature data loggers (Onset Computer Corporation: HOBOS) were distributed throughout the cove (Fall 2013, $n = 6$; Summer 2014, $n = 7$) on the seafloor to record water temperature (resolution = $0.14^{\circ}C$ at $25^{\circ}C$) every 15 min (Fig. 1B).

Batoid geo-position data by species were plotted on a geo-referenced map of BFC and analyzed using ArcGIS (ArcMap vers. 10.2). To characterize the spatial areas used by the

different species, a 95% kernel utilization distribution (KUD) was calculated incorporating all positions determined for each species over the entire survey time period (all 2013 and 2014 surveys) (Worton 1987). The percent area overlap of the three species for each season was compared to take temporal differences of distribution into account. The KUDs of each species were then layered to determine the percent area overlap of the three species.

To quantify batoid substrata selection, a benthic habitat map of BFC was created by doing separate snorkeling surveys taking GPS points every 2 m. We then took those GPS points and interpolated polygons using ArcGIS to classify the habitat into hard and soft substrata (resolution approx. 5 m) (Fig. 1C). The habitat was classified into two rocky substrata categories: bare rock and rock with giant kelp (*Macrocystis pyrifera*); as well as two soft sediment substrata categories: fine-sand and vegetated-sand (with low relief macroalgae and seagrass). A habitat selection index (HSI) was used to determine each species selection for a specific substrata type. The HSI calculation was done for each species over each available substratum to create a species-specific analysis (pooling all surveys from both seasons). For each species, the HSI was calculated by dividing the proportion of positions within each substrata type by the proportion of that substrata type available in the survey area (2.73 ha). The numerator proportion was calculated by dividing the number of positions of a species within a substrata type (e.g., bat rays in fine-sand) by the total number of positions of that species in all substrata types. The denominator proportion was calculated by dividing the total area of a substrata type available (e.g., fine-sand) by the total survey area (2.73 ha). An HSI value of one or greater indicates selection, whereas a value less than one indicates non-selection of that habitat (Winter and Ross 1982). Chi-square tests in R v. 3.2.1 (R Foundation for Statistical Computing, Vienna, Austria) were used to determine if the elasmobranchs selected substrata disproportionally from what was available in the survey area within BFC.

Temperature interpolations were done using the Inverse Distance Weighted (IDW) technique in ArcGIS (Zimmerman et al. 1999). Interpolated temperature data collected during the surveys visually showed no clumped aggregation patterns. However, Fall 2013 and Summer 2014 seasonal distributions were centered around the southwest corner of BFC where daily temperatures would reach their warmest. Therefore, to compare seasonal temperature selection and to determine if the warmest daily temperatures were driving distributions of batoids in BFC, we used daily (9:00 – 17:00 hrs) maximum seafloor water temperatures. To compare batoid abundance with daily maximum temperatures, the maximum interpolated temperature of each individual's location was recorded and grouped into corresponding 0.25°C temperature bins. To quantify disproportional temperature use, a fishnet grid was created with ArcGIS that consisted of 5 m² cells. Mean maximum sea floor water temperature and number of individuals of each species were extracted from each cell. Cells of all surveys were pooled together to construct histograms for each batoid in R to determine how each species selected temperature compared to what was available in the survey area. Chi-square tests were used to determine if the elasmobranchs significantly selected temperatures disproportionally from what was available in the cove.

Mean maximum sea floor water temperature, major substratum type (> 50%), and the total number of individuals of each batoid were extracted from each grid cell. Hurdle models were then conducted in R to statistically quantify how the environmental variables predicted abundance of each species. The hurdle model is a two part model; 1) a binomial probability model that determines presence or absence of individuals of a species in a grid cell, then 2) a truncated count data distribution, which describes the positive outcomes, or presence of individuals, based on substrata type and temperature (Cameron and Trivedi

2013). To determine what variables affected presence of each species within a grid cell, a logistic regression was run with a binomial distribution of either presence or absence of individuals within a cell. Once the first “hurdle” was crossed, the second step of the hurdle model used general linear models (GLMs) to identify which environmental variable best described the abundance of individuals. Only substrata types that were selected by the elasmobranchs were included in the GLMs to improve our ability to determine a difference in elasmobranch abundance among selected substrata types. An additional GLM was run with bat ray positions from Fall 2013 and Summer 2014 pooled together to compare across seasons.

Results

The daily mean (\pm SD) abundances of batoids counted per survey during Fall 2013 was 38 ± 29 bat rays, 18 ± 10 shovelnose, and 26 ± 16 round stingrays. The mean (\pm SD) daily abundances counted during Summer 2014 was 19 ± 13 bat rays, and 1 ± 1 shovelnose. During Fall 2013, the resting distribution of all three batoids shared an overlapping area of 0.045 ha, only 1.6% of the total survey area (2.73 ha). During Summer 2014, the resting distribution of bat rays and shovelnose had an overlapping area of 5×10^{-5} ha (only 2 individuals overlapped throughout the summer). Due to the absence of round stingrays and low abundance of shovelnose during Summer 2014, positional data for both seasons were pooled for KUD analysis. The resulting resting distribution area of the three batoids from all surveys encompassed a total area of 1.02 ha, 37% of the total surveyed area (2.73 ha). However, the overlapping distribution area of all three batoids encompassed 0.087 ha, comprising approximately only 3% of the surveyed area of BFC (2.73 ha), indicating some segregation by species groups (Fig. 2).

Out of the four substrata types available in BFC, batoids were only found resting in the two soft substrata: fine-sand and vegetated-sand. Bat rays ($X^2 = 288.76$, $df = 3$, $p < 0.001$), shovelnose ($X^2 = 132.76$, $df = 3$, $p < 0.001$), and round stingrays ($X^2 = 147.47$, $df = 3$, $p < 0.001$) all selected their substrata disproportionally from what was available in BFC. All three species were found to select fine-sand substrata, while only bat rays showed additional selection of vegetated-sand (HSI values: bat rays: fine-sand = 1.59, vegetated-sand = 1.19; shovelnose: fine-sand = 2.01, vegetated-sand = 0.25; round stingrays: fine-sand = 2.03, vegetated-sand = 0.21) (Fig. 3).

Daily temperature fluctuations within the study area never exceeded more than 3°C. The highest seafloor temperatures for Fall 2013 and Summer 2014 were 19.25°C and 20.75°C, respectively. During Fall 2013, the highest abundance of positions for all three batoids was between 18.00-18.25°C (Chi-square test: $X^2 = 190.3$, $df = 25$, $p < 0.001$) (Fig. 4). Bat rays displayed a random distribution during Fall 2013 where not all individuals were observed resting in the warmest waters; however, when daily maximum temperatures reached 20°C in Summer 2014, bat rays demonstrated a clumped distribution pattern (Fig. 5). All three batoids used water temperatures disproportionally to what was available (bat rays: $X^2 = 174.96$, $p < 0.001$; shovelnose: $X^2 = 60.6$, $p < 0.001$; round stingrays: $X^2 = 51.87$, $p < 0.001$) (Fig. 6).

Results of the hurdle model showed that in Fall 2013, temperature predicted the presence of bat rays ($p = 0.001$), but substrata type did not ($p = 0.09$). While temperature determined presence, neither substrata ($p = 0.49$) nor temperature ($p = 0.35$) predicted bat ray abundance. In Summer 2014, both temperature ($p < 0.001$) and substrata type ($p < 0.001$) predicted the likelihood of bat ray presence, while neither substrata type

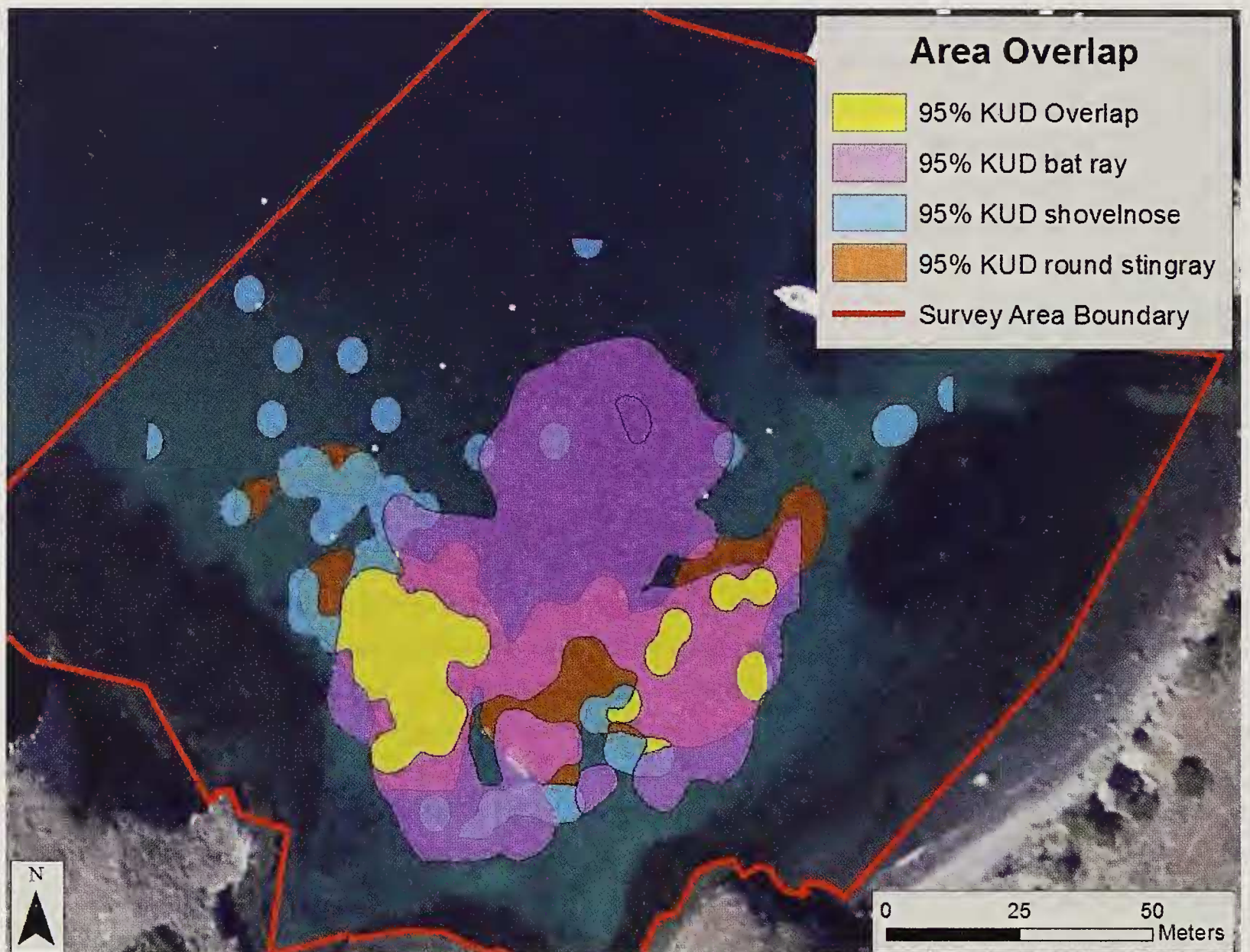


Fig. 2. Map of the 95% kernel utilization distribution (KUD) areas for bat rays, shovelnose, and round stingrays for all positional data from both Fall 2013 and Summer 2014. The yellow area indicates the overlap of KUD areas for all three species for both survey seasons (37% of total area used by the batoids).

($p = 0.07$) nor temperature ($p = 0.93$) predicted abundance. However, when all positions for bat rays from both seasons are pooled together, temperature predicted both presence ($p < 0.001$) and abundance of rays ($p = 0.04$), while substrata type did not (presence: $p < 0.11$; abundance: $p = 0.75$) (Fig. 7A). For shovelnose, substrata type predicted both presence ($p < 0.001$) and abundance ($p < 0.001$), while temperature did not predict either presence ($p = 0.16$) or abundance ($p = 0.97$) (Fig. 7B). Round stingray presence was influenced by both temperature ($p < 0.001$) and substrata type ($p < 0.001$), while neither substrata type ($p = 0.42$) nor temperature ($p = 0.34$) influenced abundance (Fig. 7C).

Discussion

Our study assumed the batoid species lying on the seafloor had chosen suitable habitat for them to rest or take refuge. Smaller species or individuals could potentially be more at risk causing them to take refuge by burying within the substrata more often than larger individuals. Fine-sand substrata likely provides more suitable burying habitat for batoids, whereas vegetated-sand substrata alternatively provides low-relief vegetation for crypsis, and potentially higher benthic in- and epi- faunal densities (Thrush et al. 1991; Cross and Curran 2000). While all three species were found resting on both soft substrata types available (fine-sand and vegetated-sand), fine-sand was selected by all three species, whereas bat rays were the only one of the three species to additionally select for vegetated-sand. Round stingrays and shovelnose are light brown to gray in color and can blend in while

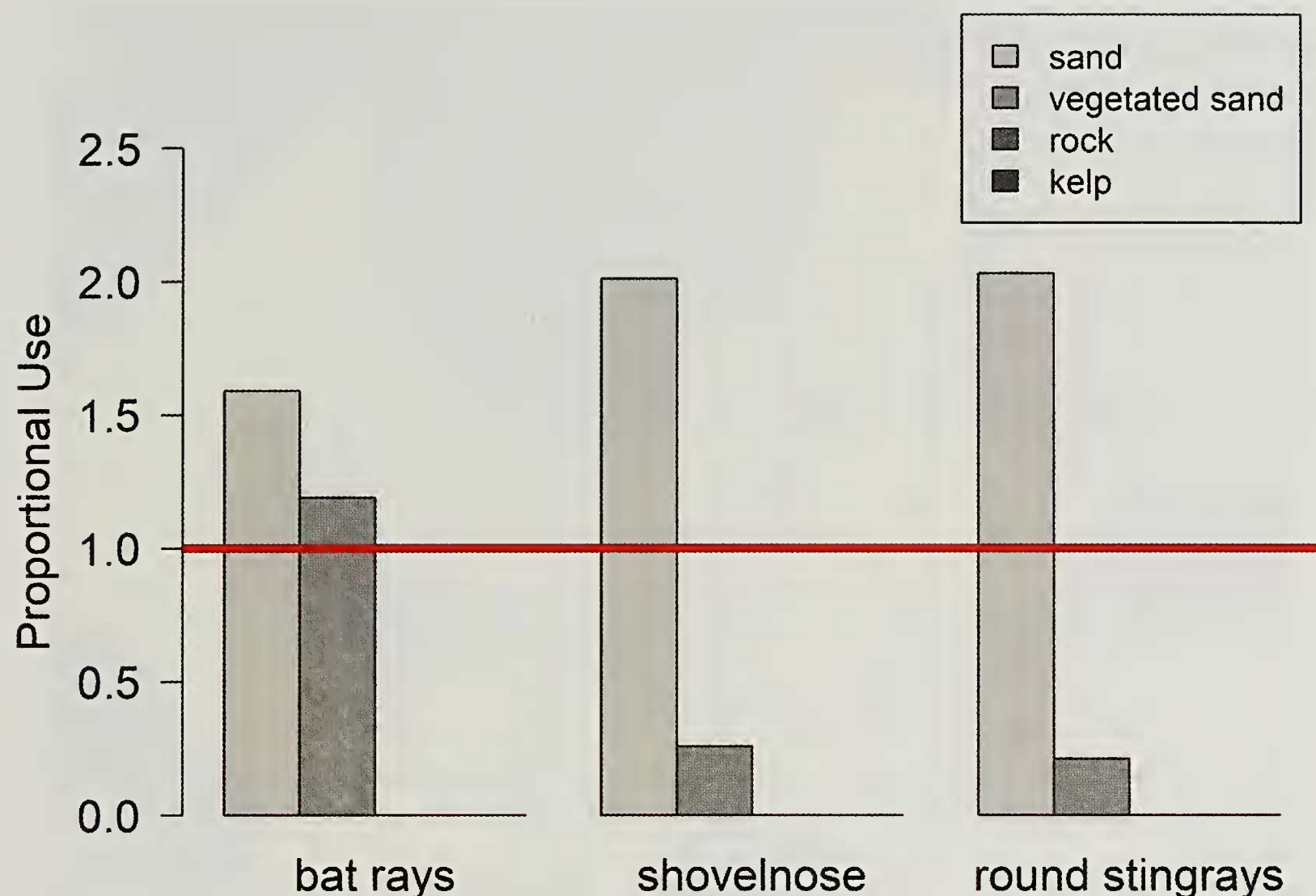


Fig. 3. Habitat selection index (HSI) for substrata types for the three batoid species surveyed in both Fall 2013 and Summer 2014. The red horizontal line designates the HSI selection value of 1.

partially buried or resting on fine-sand substrata. Bat rays on the other hand tend to be darker on their dorsal surface, which could explain why juveniles were observed buried in shallow, fine-sand areas, while larger bat rays were observed resting on the vegetated-sand substrata while at rest.

Within species, body size may have influenced substrata and temperature selection. While size of each resting individual was not recorded, estimated age classes including juvenile bat rays, juvenile shovelnose, and all round stingrays were typically found in shallower, warmer, fine-sand substrata, while adult shovelnose and adult bat rays were found in relatively deeper, cooler, vegetated-sand substrata. Previous studies have demonstrated ontogenetic shifts in thermal preference where larger individuals tend to prefer cooler water temperatures (Magnuson et al. 1979; Hopkins and Cech 2003), which may explain the size stratified distributions we observed among the three species.

Because of varying body sizes, these species likely differ in their thermal sensitivities; however, it is unclear how daily temperature ranges influenced fine-scale temperature selection. There was no overlap between Fall 2013 (17.50 – 19.25°C) and Summer 2014 (19.50 – 20.50°C) temperatures, and daily ranges never exceeded more than 3°C. Interestingly, all three species were most abundant across a narrow temperature range (18.00 – 18.25°C) during Fall 2013. This suggests that daily temperature ranges may have provided a thermal refuge by allowing these species to rest for longer periods of time, potentially allowing a physiological advantage (Bernal and Lowe 2015). However, based on the variation in daily abundances and distributions, we hypothesize that all three species periodically leave BFC (i.e., for foraging, other preferred environmental conditions); however, the temporal and spatial scale of these patterns (i.e., diel, seasonal) may vary by species.

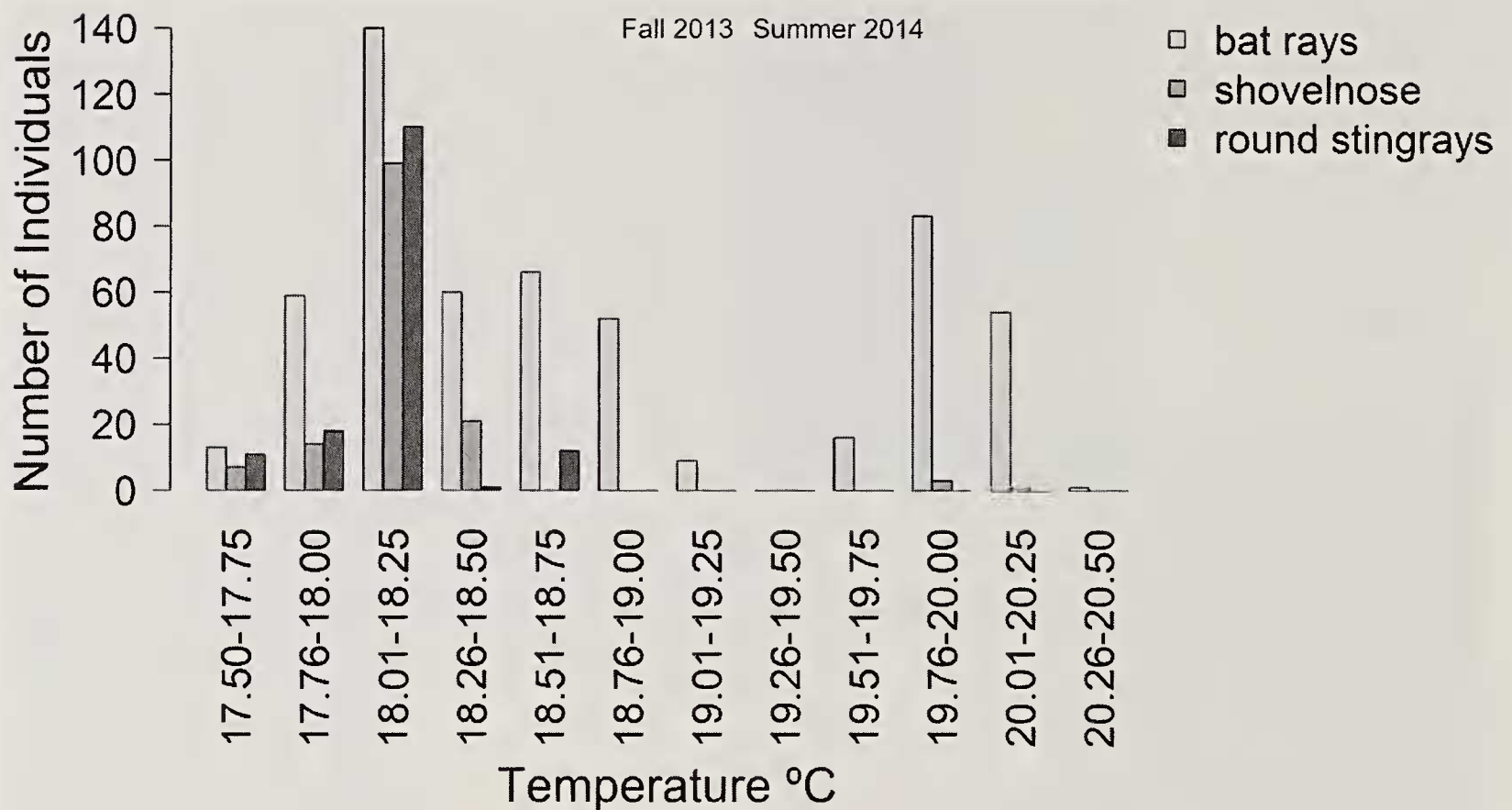


Fig. 4. Pooled extracted temperature data from the daily maximum inverse distance weighted interpolations (IDWs) for all species from all surveys. Summer 2014 temperature ranges are shaded in gray.

While this study was done during warmer seasons (e.g., Summer and Fall), colder seasons (e.g., Winter and Spring) might result in different temperature selection and distribution patterns. For instance, during Summer 2014, there were higher densities of bat rays in areas where daily maximum seafloor water temperatures reached 20°C. This seasonal peak in temperature may act as a threshold for adult bat rays where there is an increased benefit to metabolic performance or reproduction (i.e., shortening gestation) (Wallman and Bennett 2006; Jirik and Lowe 2012). Martin and Cailliet (1988) found in Elkhorn Slough, California, ovulating females were only present during summer months. Therefore, the observed summer bat ray aggregations could have been mostly females seeking a reproductive advantage, similar to leopard sharks also found in BFC (Hight and Lowe 2007). We could not easily determine the sex of resting individuals during surveys for this study, so the ratio of females to males in these summer aggregations in BFC is unknown.

Thermal preferences and sensitivities among the three batoid species may explain some of the heterospecific variation in daily abundances and spatial distributions. Bat rays can be extremely sensitive to temperatures outside 14-20°C and have a high unacclimated metabolic Q_{10} of 6.81 (Hopkins and Cech 1994). During daytime observations, bat rays in BFC may have been “shuttling” between habitats (i.e., warmer, fine-sand vs. colder, vegetated-sand) to optimize net energetic gain according to the “hunt warm – rest cool” hypothesis (Matern et al. 2000; Bernal and Lowe 2015). Round stingrays, in contrast, are the smallest of the three batoid species, implying they may have the lowest thermal tolerance, though their thermal sensitivity or metabolic Q_{10} s have not yet been quantified (Hoisington and Lowe 2005). Seal Beach, California is a location where high densities of round stingrays seasonally aggregate because of the warm water effluent from the San Gabriel River (Babel 1967; Hoisington and Lowe 2005; Vaudo and Lowe 2006; Jirik and Lowe 2012). While stingrays are present throughout the year at Seal Beach, abundance varies with season and residence time is only approximately two weeks (Hoisington and Lowe 2005; Vaudo and Lowe 2006). Because of these patterns, it has been proposed that

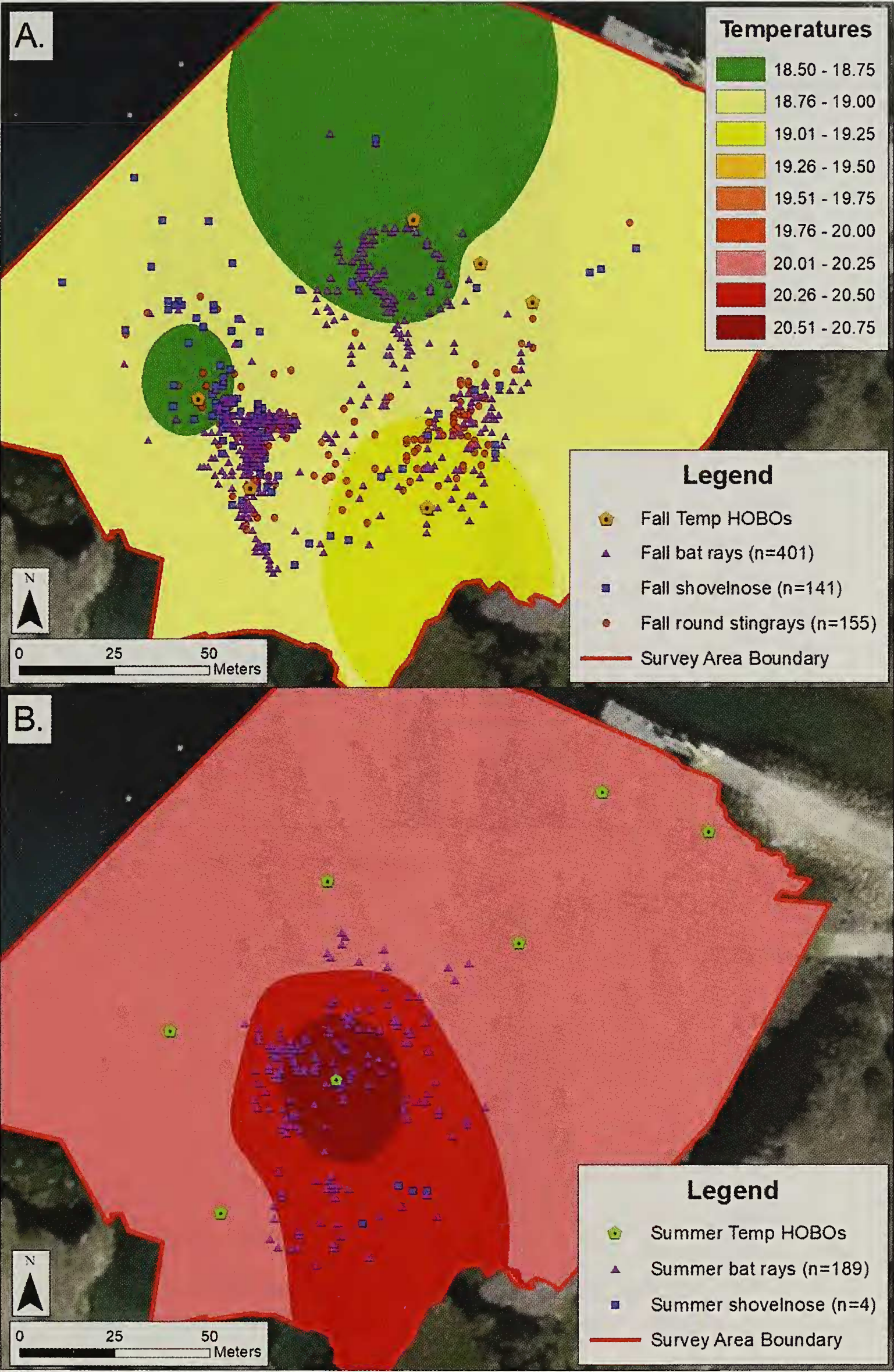


Fig. 5. Temperature IDW interpolations for the average maximum temperatures for both Fall 2013 (A) and Summer 2014 (B) survey seasons. There was no overlap between Fall 2013 (17.50 – 19.25°C) and Summer 2014 (19.50 – 20.50°C) temperatures. Positional estimates observed for each species are presented for each respected season, as well as locations of temperature data loggers for each season.

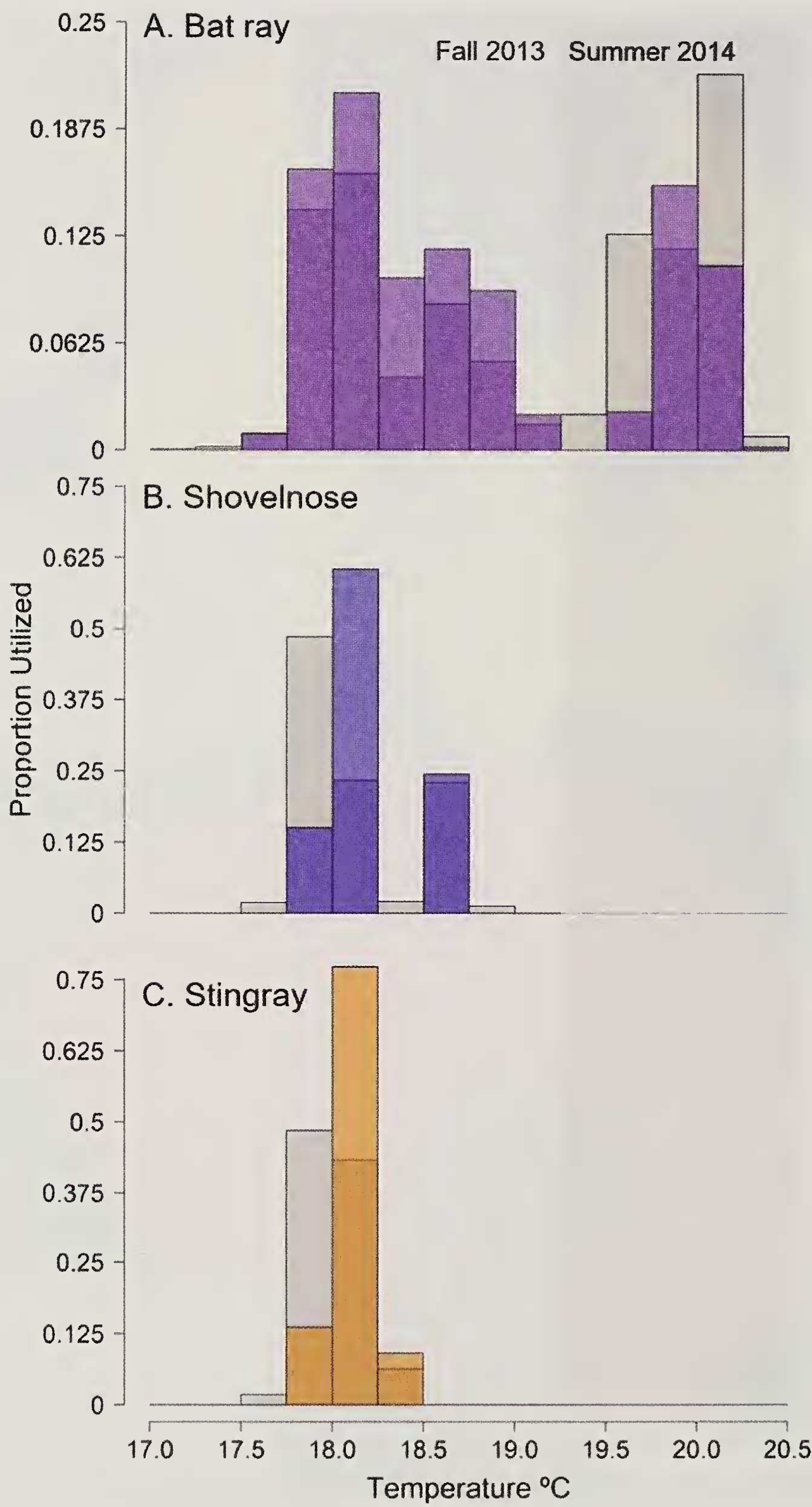


Fig. 6. Disproportional temperature use for all three batoid species for both seasons (shaded region shows Summer 2014). Gray bars represent temperatures available, whereas colored bars represent the proportions of temperatures used by individuals.

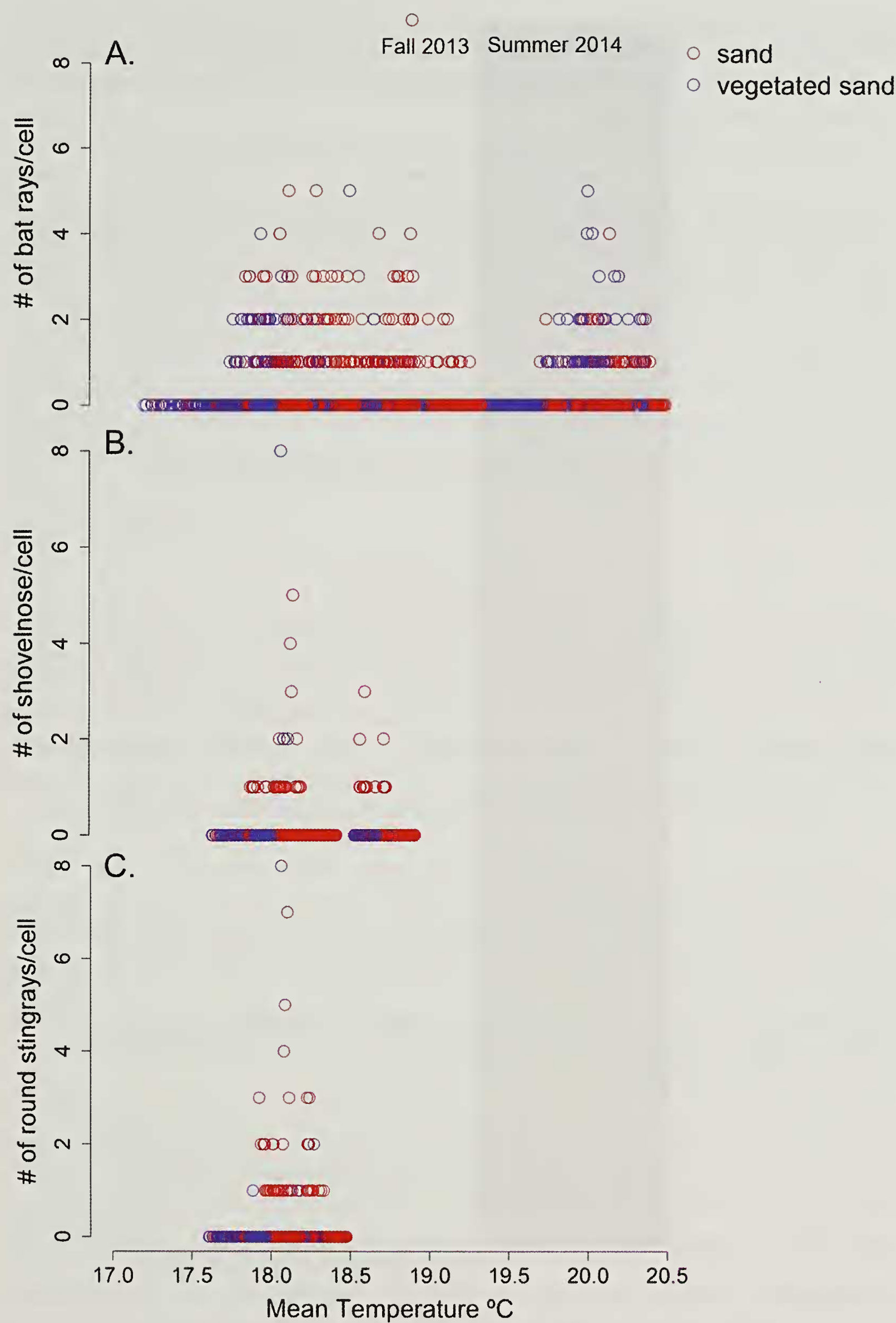


Fig. 7. General linear model results for bat rays (A), shovelnose (B), and round stingrays (C) for both Fall 2013 and Summer 2014. Substrata type is indicated by color, red denotes fine-sand and blue denotes vegetated-sand.

these Seal Beach aggregations may serve some seasonal reproductive benefit (Mull et al. 2008; Jirik and Lowe 2012). Likewise, the round stingrays aggregating in the present study may also be seeking a reproductive advantage by seeking out warm waters with preferred substrata for refuge while at rest.

Surprisingly, temperature did not influence the presence and distribution of shovelnose, whose thermal sensitivity and metabolic Q_{10} s have also not yet been quantified. Farrugia et al. (2011) conducted a comprehensive study of shovelnose movements and habitat use in the Bolsa Chica Full Tidal Basin (BCFTB) and found shovelnose prefer temperatures around 22°C. In contrast to BFC, the BCFTB is a shallow estuarine environment that has greater daily changes (12 – 30°C) in temperature compared to BFC (Espinoza et al. 2011; Freedman et al. 2015; Freedman et al. 2017). Since 22°C was rarely observed in BFC, one might expect shovelnose to instead select for the warmest possible temperatures; however, that was not the case. There is growing evidence that shovelnose may be more migratory than previously thought; therefore, it is possible they are less responsive to temperature than the other two species, and instead prioritize other environmental variables, or social aspects of aggregations, that we did not measure in this study (Espinoza et al. 2011; Nosal et al. 2014; Freedman et al. 2017).

Our Summer 2014 survey season was the beginning of the 2014 – 2016 El Niño Southern Oscillation (ENSO) event, which are known to affect distribution patterns and geographical ranges of many temperate fishes. This could potentially explain why there was no overlap in seasonal temperatures, and why abundances and distributions of the three species differed between the two warm seasons (e.g., Fall and Summer). For instance, shovelnose had the lowest mean daily abundances in Fall 2013, and only a few occurrences during Summer 2014. Farrugia et al. (2011) found shovelnose to be non-philopatric which would explain the high variability of shovelnose presence during our study. Additionally, there were no round stingrays present in Summer 2014, possibly due to reduced prey populations, or because ENSO conditions provided suitable resting conditions elsewhere.

Our study investigated what we hypothesized to be the two most important environmental variables that would drive heterospecific aggregations. While substrata type and temperature did influence batoid habitat selection decisions, other environmental variables such as depth, tidal height, salinity, and dissolved oxygen could additionally effect where these species choose to rest. For example, because batoids are dorso-ventrally flattened, they may be able to use tidal flows for transportation (Teaf 1980; Smith and Merriner 1985). Round stingrays have been shown to exhibit movement patterns consistent with daily tides (Vaudo and Lowe 2006), yet bat rays demonstrated movements correlated with temperatures but not tides (Matern et al. 2000).

Additionally, while our study did not measure any social interactions or behaviors among the three species, we are not discounting sociality as one of the potential reasons for batoid aggregations. Semeniuk and Dill (2006) found instead of relying on others as evidence of suitable resting conditions, batoids may actively seek out resting partners for other benefits that aggregating can provide. For instance, smaller, more susceptible individuals (e.g., round stingrays, juvenile bat rays) may aggregate to increase vigilance and to flee in groups when necessary, as opposed to individually. It is possible that the heterospecific aggregations we observed are formed because more susceptible species can take advantage of greater sensory capabilities of the other species (Semeniuk and Dill 2006). In addition, since these batoid species are benthic foragers, they may use social cues (both con- and heterospecific) to help find prey along the seafloor. While we assumed the individuals recorded for this study were at rest, these batoids could have also been waiting to detect prey along

the seafloor (e.g., water jets from siphons) (Matern et al. 2000). Understanding the relationship between foraging and habitat selection of batoid species is ecologically important since their foraging behavior can result in high sediment turnover and altered invertebrate communities.

Conclusions

When faced with choosing a resting place, bat rays, shovelnose, and round stingrays must balance tradeoffs between substrata type (i.e., soft sediment for refuge and potentially prey-rich environments for foraging) and temperature (i.e., physiological advantages). It is important to understand how meso-level predators such as batoids respond to these variables to make predictions as to how changing ocean temperatures and coastal urbanization may affect the diel and seasonal distribution patterns and behaviors of these batoid species. Resource managers can use this information to better protect these aggregating, K-selected species in their preferred habitats. Moving forward, research should focus on environmental and social aggregation mechanisms of batoids to create the most effective approach for understanding habitat selection decisions and implementing proper protection and restoration plans.

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